

Genetic Study of the Population of Tenerife (Canary Islands, Spain): Protein Markers and Review of Classical Polymorphisms

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ABSTRACT Data on six protein polymorphisms (19 alleles) from the human population of Tenerife are presented and discussed along with other classical markers in relation to the origin of the Canarians. Genetic influences from three population groups were considered: the Iberians, and the Berbers and non-Berbers (Arabs) from north Africa. The systems examined show the Tenerife population lies within the limits of variation described for various Iberian groups, with a slight tendency towards the characteristics of north African populations. When blood groups, red cell enzymes and serum protein data were considered, the similarity of the Canary population to Iberians seems strengthened (70% estimated contribution of Iberian peninsula genes to the present-day Canarian pool), while some relation with north African groups is shown. Genetic distances between Canarians and Arabs and Canarians and Berbers are lower than those between the two north African groups, indicating a relative and comparable contribution of each to the present-day gene pool of the Canarian population. The Arab contribution could be attributable to the slaves who were introduced to these islands after the conquest in the 15th century, while the Berber contribution could be the remnants of the extinct aboriginal peoples of the islands (Guanches) or a more recent immigration due to slavery. Genetic data do not allow us to distinguish between these two possibilities. *Am. J. Phys. Anthropol.* 102:337-349, 1997.

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Tenerife, the largest island in the Canaries archipelago, lies in the Atlantic Ocean, off the northwest coast of Africa. In spite of their geographical location, the Canary Islands have been part of Spain since 1479 when the Treaty of Alcáçovas recognized Spanish sovereignty over them. Known since the 1st century B.C., the archipelago was visited by various medieval navigators including Arabs, Genoese, Majorcans, Portuguese, and French. Nevertheless, its conquest began in the 15th century, first tried

by Portuguese and later by Normans with the support of the Kings of Castile. The conquest was a hard enterprise: Lanzarote was occupied in 1402, but Tenerife resisted until 1496.

The genetic background of the present Canary islanders has long been a matter of

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interest for anthropologists. The aboriginal population of the Canary Islands were known as the Guanches, although strictly speaking, the word is of Berber origin, meaning "autochthonous" and refers solely to the inhabitants of Tenerife (Onrubia Pintado, 1987). The conquerors found the Canary Islands widely inhabited by the Guanches who were at an advanced Neolithic stage of development. Various hypotheses concerning the origin of the Guanches have been propounded. Anthropometric data seem to relate them to the palaeolithic Cromagnon (Verneau, 1887; Fischer, 1931) or to the robust Mediterranean peoples (proto-Mediterranean or Eurafrikanid; Fusté, 1959, 1962; Schwidetzky, 1963) both of which would probably have migrated to the Canary Islands from northwest Africa. Linguistic studies identify certain links with Berber (Abercromby, 1917) and other languages of north Africa (Wolfel, 1955). Alphabetic inscriptions comprising Libyco-Berber characters found in the Canary Islands (coll. Musée de l'Homme, Paris) would seem to confirm links between Guanches and north Africa. During and after the conquest, many Guanche people were killed or deported as slaves to Europe or the near Madeira Islands (Crosby, 1986). The archipelago was initially repopulated with Norman peasants and later by the Spanish who converted the surviving aborigines to Christianity and intermarriage became common (Wolfel, 1930). At a later date, slaves from the north and west African coast were brought to work the land.

Today's Canary population is a mixture of all these peoples. Their genetic contribution has been studied with blood group data (Roberts et al., 1966), some serum proteins such as haptoglobin (HP), vitamin-D binding protein (GC) and immunoglobulin (GM; Kahlich-Könner et al., 1969), and dermatoglyphics (Fusté, 1965). All these studies highlight the similarity between the Canarian and Spanish populations, and show certain affinities with groups from north and west Africa. A more recent set of studies based on enzyme systems (Morilla et al., 1988; Pinto et al., 1994) estimates genetic contributions to have been the following: Spanish, 70%; Berber, 20%; and Black African, 10%. The present study describes, for

the first time, data gathered on transferrin (TF), GC subtypes, protease inhibitor alpha-1-antitrypsin (PI), orosomucoid type I (ORM1) and plasminogen (PLG) and HP. The latter has been previously studied by other authors in other Canarian samples. These polymorphisms have been studied extensively worldwide, except ORM1 and PLG, for which population studies have not been so widespread. Tenerife people can be considered to be representative of the general Canarian population due to the internal pattern of migration within the archipelago from the smaller to the larger islands (Tenerife and Gran Canaria).

MATERIALS AND METHODS

Blood specimens from 108 individuals were collected in the Hospital of the University of La Laguna (Tenerife). One of us (E.G.-R.) controlled the sampling: only unrelated donors whose grandparents (all four) were natives of the Canary Islands were considered. Sera was removed and stored at -40°C until testing.

Common HP types were analyzed in polyacrylamide gel electrophoresis with Tris-glycine buffer (pH 9.0) and visualized using the increase in peroxidase activity of haptoglobin-haemoglobin complexes. The phenotypes of TF, GC, PI, ORM1, and PLG were determined by isoelectric focusing (IEF) on thin-layer polyacrylamide gels according to standard laboratory procedures (Cleve et al., 1992; Moral et al., 1994b). Sera treatment was carried out on TF and PLG only prior to IEF: TF subtyping was performed from sera diluted one-fifth in a 0.25% ferrous ammonium sulphate solution and kept overnight at 4°C , and for PLG analysis, 10 μl serum were desialyzed with 10 μl neuraminidase (*Clostridium perfringens* 1 U/mg, Boehringer M.) at 37°C overnight. TF, GC and PI subtypes were demonstrated by protein fixation with a sulfosalicylic acid solution and subsequent staining with Coomassie Blue in the case of TF and PI. For the detection of PLG, gel immunofixation was carried out with a 1:4 diluted monospecific PLG antiserum (Behring-Werke, Marburg, Germany). ORM1 and PLG bands were detected by silver staining.

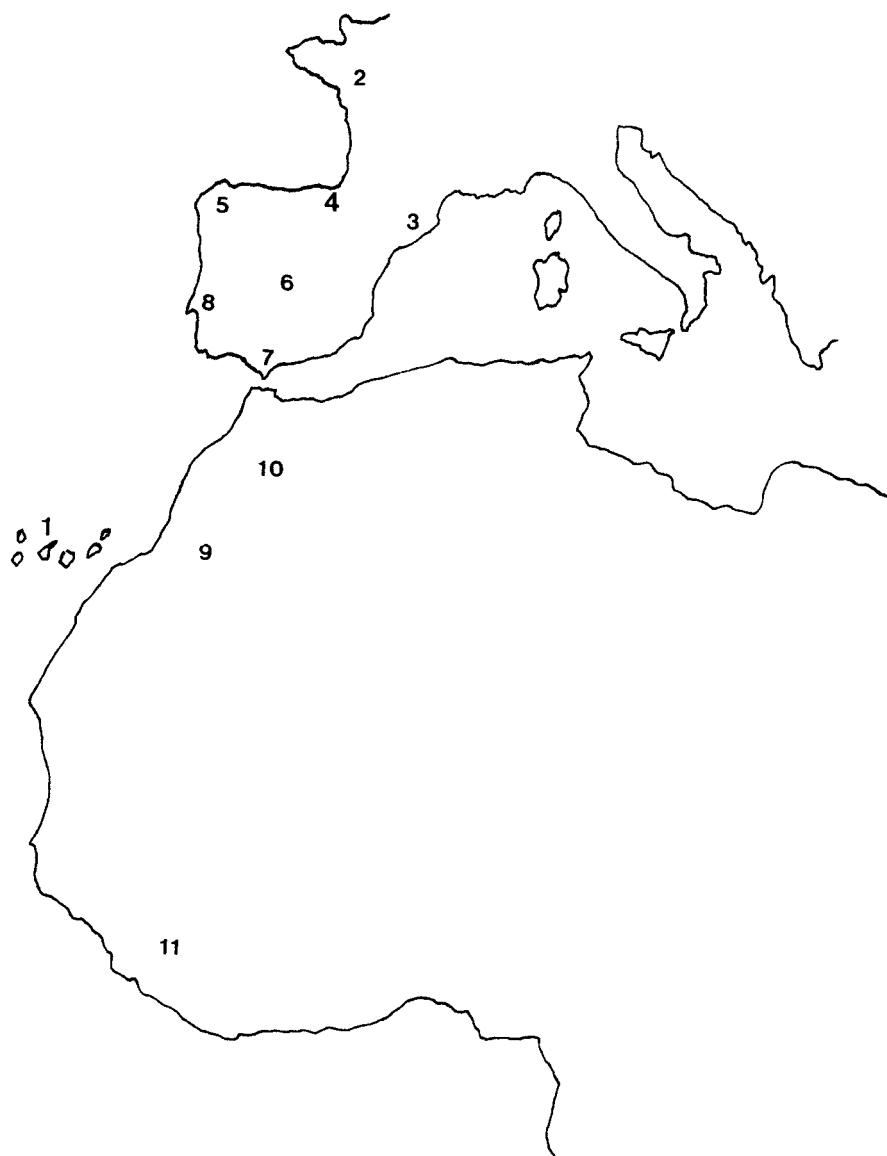


Fig. 1. Geographic location of Tenerife and populations used for comparison. 1: Tenerife Island, TEN; 2: France, FRA; 3: Catalonia, CAT; 4: Basque Country, BAS; 5: Galicia, GAL; 6: Central Spain, CEN; 7: Andalu-

sia, AND; 8: Portugal, POR; 9: north African Berbers, BER; 10: north African Arabs, ARA; 11: sub-Saharan west Africa, WAF.

Maximum likelihood allele frequency estimates were computed and goodness of fit to Hardy-Weinberg equilibrium was evaluated by the chi-square test. Protein frequency distributions in Tenerife were discussed in relation to the variation range of these markers in European and north African populations.

To assess genetic affinities between Canarians and other populations, data on several groups from southwestern Europe, north Africa (Berbers and non-Berbers) and west Africa were selected from the literature. These samples were chosen because history and geographic proximity suggest possible connections to the Canary Islands. Geo-

graphic locations are indicated in Figure 1. First, comparisons were made using the serum protein data presented here, and then a global picture of the genetic relationships between Canarians and the above populations was considered by including data on additional classical polymorphisms. Thus, published data on blood groups (ABO, Rh, MNSs, and Duffy) red cell enzymes (acid phosphatase [ACP-1], acetylcholinesterase [EsD], glyoxalase I [GLOI], and phosphogluconate dehydrogenase [PGD]) were used together with those on serum proteins (HP, TF, GC, and PI). PLG and ORM1 were not included in the global analysis, because information was not available for all populations.

Genetic distances were computed by the GENDIST program in the version 3.5c of the PHYLIP package (Felsenstein, 1989) according to the methods of Cavalli-Sforza and Edwards (1967), Nei (1972), and Reynolds et al. (1983). Reynolds' distances

$$(d = -\ln(1 - \theta)),$$

where θ is the coancestry coefficient) were selected because these estimates are proportional to the time since the populations diverged when the main differentiating agent is genetic drift. This evolutionary force seems to drive differentiation in human populations, especially at a microgeographical level (Cavalli-Sforza et al., 1994). From genetic distances, a neighbor-joining tree (Saitou and Nei, 1987) was constructed using the NEIGHBOR program of the same package. This method, which does not assume a constant evolutionary rate, finds the shortest tree that provides a faithful representation of the relationships contained in a distance matrix. The reliability both for genetic distances and tree was assessed by the bootstrap resampling method (Efron, 1982). One hundred resamples were drawn with replacement from the original allele set and the standard deviation of these 100 distances was taken as an estimation of genetic distance standard errors. The same bootstrapped distance matrices were used to build 100 trees. The number of times that a particular subgroup of populations appeared joined was counted using the CONSENSE program in PHYLIP3.5c, and was given as a percentage of occurrences for each node in

topology of the original tree. This proportion can be interpreted as an estimate of the consistency of the different population clusters on the tree. In spite of the wide use of Felsenstein's rule that a cluster is supported significantly if it appears in at least 95% of bootstrap trees, which bootstrap percentage indicates statistical significance remains an unresolved question because bootstrap is not a significance test (Brown, 1994). On the other hand, since bootstrap generally is applied to test if a given cluster is better supported than all possible alternatives, which is equivalent to asking whether or not there is significant evidence that the cluster appears in more than 50% of all bootstrap trees, values larger than 50% are considered as indication of statistical support. Genetic relationships among populations were also measured through principal-component analysis (Cavalli-Sforza and Piazza, 1975).

Admixture levels were estimated from genetic distances according to Cavalli-Sforza's formula

$$m = 1/2 + (f_{BM} - f_{AM})/(2*f_{AB}),$$

where f_{AB} is the F_{ST} distance between ancestors and f_{AM} , f_{BM} , the distances between each of the two ancestors and the mixture (Cavalli-Sforza et al., 1994).

RESULTS

Protein data

Phenotype and allele frequencies for the six proteins in the population of Tenerife are reported in Table 1. Phenotype distributions show no significant deviation from Hardy-Weinberg equilibrium for all the loci examined. No rare alleles are found, except for one carrier of TF*D allele. Mean heterozygosity per locus (direct-count estimate) is 0.486 ± 0.033 . Data on the same systems analyzed from Iberian peninsula, north Africa, and west Africa are summarized in Table 2 for comparative purposes. Chi-square heterogeneity values between Tenerife and several population groups from these geographical regions are indicated in Table 3.

HP system. Results in Tenerife are similar to those observed in earlier studies on the Canary Islands (Fusté, 1965; Pons et al., 1968), but differ significantly from data re-

TABLE 1. Phenotype and allele frequency distribution in the Tenerife population, Canary Islands

Phenotype	Observed	Gene frequencies		Phenotype	Observed	Gene frequencies	
<i>HP</i>				<i>PI</i>			
1	23			M1	32		
21	48	HP*1	0.452 ± 0.034	M1M2	23		
2	33	HP*2	0.548 ± 0.034	M2	5		
Total	104			M1M3	12		
<i>TF</i>				M2M3	2	PI*M1	0.528 ± 0.033
C1	57	TF*C1	0.738 ± 0.030	M3	0	PI*M2	0.190 ± 0.026
C1C2	35	TF*C2	0.233 ± 0.029	M1M4	1	PI*M3	0.106 ± 0.020
C2	7	TF*C3	0.024 ± 0.010	M2M4	0	PI*M4	0.023 ± 0.010
C1C3	5	TF*D	0.005 ± 0.004	M3M4	1	PI*S	0.144 ± 0.023
C1D	1			M4	1	PI*Z	0.009 ± 0.006
Total	105			M1S	14		
<i>GC</i>				M2S	4		
1F	2			M3S	8		
1F1S	18	GC*1F	0.124 ± 0.022	M4S	1		
1S	43	GC*1S	0.624 ± 0.033	S	2		
21F	4	GC*2	0.252 ± 0.029	M1Z	—		
21S	27			M2Z	2		
2	11			Total	108		
Total	105			<i>ORM1</i>			
<i>PLG</i>				F	41		
A	54			FS	56	ORM*F	0.639 ± 0.032
AB	47	PLG*A	0.745 ± 0.030	S	11	ORM*S	0.361 ± 0.032
B	3	PLG*B	0.255 ± 0.030	Total	108		
Total	104						

ported in Kahlich-Könner et al. (1969). In our sample, the frequency of HP*1 allele (0.452) is close to the highest values found on the Iberian peninsula (Table 2) or in other European groups. That value is similar to those described in some North Africans such as Tuaregs from Algeria (Constans et al., 1978) and from Mali (Constans et al., 1981), Tunisians (Chibani et al., 1985) and Libyans (Walter et al., 1975), but is significantly higher than those from Bedouins and Egyptians. HP*1 allele frequencies in west Africa (averaging around 70%) are significantly higher than in Tenerife (Table 3).

TF system. Low TC*C1 and high TF*C2 allele frequencies were observed in Tenerife in comparison to Iberian peninsula (Table 2). The same is true in relation to other Europeans (TF*C1: 0.75–0.90, TF*C2: 0.10–0.20 [for a review see Kamboh and Ferrell, 1987]). TF*C3 was observed in the present sample, but its frequency (0.024) falls below the European range (0.04–0.07). Remarkable differences for the frequency distribution of the TF*C genes are found with several groups from the Iberian peninsula (see Table 3). The relatively high frequency observed for TF*C2 (0.233) seems to be closer

to those reported in some north African groups (Chibani et al., 1985) or in Bedouins and Arabs from the Middle East (Cleve et al., 1992; Saha and Banerjee, 1986). However, significant differences are observed for the TF frequency distribution pattern from north Africa, and from west Africa (Tables 2 and 3). The presence of the rare TF*D variant could be evidence of a black African contribution to the gene pool. However, its very low incidence (0.005) and the fact that we could not subtype it, make any discussion of its possible source difficult. It might either indicate some admixture or represent the presence of rare genes without foreign contribution.

GC system. Only slight differences from Iberian peninsula groups are found for GC subtype distribution in Tenerife, mainly due to a high GC*1S frequency (0.624) and a low GC*2 frequency (0.252; Table 2). In general, GC frequencies in Tenerife range within European values (Kamboh and Ferrell, 1986; Piazza et al., 1989; Roychoudhury and Nei, 1988). However, a clear differentiation appeared from all African samples reviewed which show high GC*1F and low GC*2 frequencies. These differences from Berbers, Tunisians, Arabs, and Bedouins from the

TABLE 2. Variability for HP, GC, TF, PI, PLG and ORM1 among Iberian and African populations

Marker	Allele	Iberian peninsula			North Africa			West Africa		
		n ¹	Range	Extreme samples	n	Range	Extreme samples	n	Range	Extreme samples
HP	1	54	.295–.487	N Portugal ² / Basques	21	.211–.656	Egyptian Bedouins/Al- gerian Tuaregs	18	.550–.725	Ivory Coast/ Senegal
TF	C1	31	.742–.857	NW Spain/ Basques	9	.714–.764	Tunisian Berbers/ Egyptian Arabs	1	.871	Liberia
	C2		.081–.208	Basques/NW Spain		.193–.275	Egyptian Arabs/ Jordan Bedouins		.057	
	C3		.017–.070	S Spain/N Por- tugal		.031	Egyptian Arabs		.000	
	B		.000–.032	Several/Central Spain		.006–.007	Egyptian Arabs/ Tunisian Ber- bers		.008	
	Others		.000–.005	Several/S Spain		.004–.015	Jordan Bedouins/ Tunisian Arabs		.064	
GC	1F	43	.058–.188	NE Spain/Central Spain	5	.215–.482	Tunisian Berbers/ Algerian Arabs	1	.780	Senegal
	1S		.474–.628	Central Spain/S Spain		.446–.600	Algerian Arabs/ Tunisian Ber- bers		.115	
	2		.225–.380	Central Spain/S Spain		.015–.215	Algerian Tuaregs/ Tunisian Arabs		.053	
	Others		.000–.010	Several/Central Spain		.000–.018	Several/Algerian Tuaregs		.052	
PLG	A	9	.728–.845	W Spain/Basques	1	.641	Libyan Arabs	1	.859	Gambia
	B		.148–.241	Basques/W Spain		.309			.141	
PI	Others		.000–.031	Several/W Spain		.050			.000	
	M1	33	.538–.750	NE Spain/S Spain	4	.630–.700	Tunisian Berbers	1	.958	Liberia
	M2		.106–.204	Basques		.090–.240	Tunisian Berbers/ Tunisian Arabs		.020	
	M3		.006–.115	S Spain/NE Spain		.070–.190	Tunisian Berbers		.006	
	M4		.002–.038	NE Spain/Central Spain		N.T. ³			N.T.	
	S		.064–.149	NE Spain/NW Spain		—			.004	
	Z		.000–.023	Several/Portugal		—			.000	
	Others		.000–.005	Several/Several		.020–.040	Tunisian Berbers		.002	
ORM1	F	10	.540–.676	NW Spain/Central Spain	1	.659	Libyan Arabs	1	.618	Nigeria

¹ n is the number of studies reviewed for each main geographical area. The sources of data are the general recombinations by Mourant et al. (1976), Roychoudhury and Nei (1988), and Cavalli-Sforza et al. (1994), completed, for particular cases, with data from Moral et al. (1994b), Sebetan (1991) and Sebetan and Sagisaka (1988). Only samples in which size is greater than 99 have been considered.

² The nomenclature of Iberian samples have been simplified. The only ethnic group detached is the Basque population.

³ N.T. indicates an allele not tested.

TABLE 3. Chi-square heterogeneity values between the population of Tenerife and other populations¹

Population	HP	TF	GC	PI	ORM	PLG
Catalonia	0.63 ₁	10.62 ₄ *	3.48 ₂	20.68 ₄ ***	0.03 ₁	1.59 ₁
Basques	0.06 ₁	13.27 ₃ **	6.51 ₃	6.46 ₅	0.55 ₁	8.19 ₁ *
Galicia	0.36 ₁	9.01 ₄	2.63 ₂	24.33 ₅ ***	1.68 ₁	2.70 ₁
Central Spain	0.01 ₁	8.61 ₅	10.63 ₃ *	9.81 ₅	0.01 ₁	1.57 ₁
Andalusia	4.29 ₁ *	5.69 ₄	1.93 ₂	89.56 ₅ ***	0.59 ₁	0.01 ₁
Portugal	2.63 ₁	16.53 ₃ ***	2.33 ₂	10.10 ₄ *	1.87 ₁	2.71 ₁
France	10.27 ₁ **	14.37 ₅ *	10.63 ₃ *	24.33 ₅ ***	0.35 ₁	—
Berbers	1.54 ₁	12.68 ₄ *	9.58 ₂ **	112.89 ₅ ***	—	—
Arabs	1.13 ₁	20.45 ₃ ***	16.54 ₂ ***	250.01 ₅ ***	0.20 ₁	14.83 ₂ ***
W. Africa	38.47 ₁ ***	67.65 ₅ ***	369.37 ₃ ***	356.09 ₅ ***	0.26 ₁	7.78 ₁ **

¹ Cartographed in Figure 1. Degrees of freedom in subscript. *, ** and *** indicates 0.05, 0.01 and 0.001 significance levels, respectively.

TABLE 4. *Reynolds genetic distances and bootstrap standard errors ($\times 1,000$)¹*

	TEN ³	CAT	BAS	GAL	CEN	AND	POR	FRA	BER	ARA	WAF
Tenerife	—	13.6 (0.604)	10.0 (0.331)	10.1 (0.489)	10.8 (0.408)	21.6 (1.217)	9.4 (0.367)	15.6 (0.351)	14.9 (0.633)	25.2 (1.151)	267.5 (7.432)
Catalonia	12.2 (0.355) ²	—	4.6 (0.170)	2.4 (0.168)	4.6 (0.109)	4.5 (0.190)	14.3 (0.997)	6.1 (0.217)	18.0 (0.226)	10.8 (0.412)	244.3 (7.804)
Basques	15.2 (0.597)	10.3 (0.349)	—	5.0 (0.223)	5.2 (0.202)	13.1 (0.495)	6.9 (0.254)	10.9 (0.396)	24.2 (0.638)	22.7 (0.621)	262.6 (8.433)
Galicia	11.5 (0.254)	3.3 (0.118)	12.5 (0.522)	—	5.7 (0.193)	7.0 (0.390)	12.8 (0.674)	9.0 (0.283)	20.7 (0.355)	16.7 (0.620)	249.2 (8.018)
Centr. Sp.	11.1 (0.226)	4.2 (0.063)	9.5 (0.295)	5.3 (0.087)	—	11.5 (0.297)	10.4 (0.214)	11.1 (0.484)	16.5 (0.471)	14.4 (0.403)	224.1 (6.595)
Andalusia	14.3 (0.587)	5.3 (0.144)	11.3 (0.416)	7.2 (0.295)	7.6 (0.154)	—	21.5 (1.427)	11.0 (0.561)	23.1 (0.338)	10.9 (0.438)	259.4 (7.932)
Portugal	7.7 (0.280)	7.4 (0.400)	8.8 (0.373)	8.1 (0.352)	7.5 (0.185)	9.6 (0.548)	—	11.3 (0.534)	32.3 (0.558)	29.8 (1.410)	270.2 (6.429)
France	15.6 (0.376)	3.9 (0.105)	14.8 (0.443)	5.3 (0.136)	7.7 (0.225)	9.1 (0.299)	8.5 (0.371)	—	26.7 (0.909)	13.7 (0.214)	255.6 (5.902)
NA Berb.	26.9 (0.644)	41.0 (1.036)	42.3 (1.347)	40.5 (1.148)	40.8 (1.090)	32.5 (0.640)	40.0 (0.854)	45.9 (1.094)	—	11.3 (0.263)	217.1 (6.691)
NA Arabs	24.6 (0.753)	27.7 (0.898)	35.3 (1.049)	35.8 (0.963)	29.2 (0.967)	26.8 (0.794)	33.4 (0.961)	36.9 (1.174)	32.0 (0.813)	—	204.9 (5.251)
W. Africa	153.4 (4.909)	158.0 (4.686)	165.1 (5.476)	162.1 (4.881)	150.7 (4.367)	153.0 (4.791)	164.3 (4.718)	174.0 (4.457)	121.5 (3.859)	99.3 (3.246)	—

¹ Upper diagonal: genetic distances and standard errors based on HP, TF, GC and PI allele frequencies; lower diagonal: genetic distances and standard errors based on red cell enzymes, serum proteins and blood groups.

² Parentheses indicate the standard error of the distance estimation.

³ Abbreviations as in Figure 1.

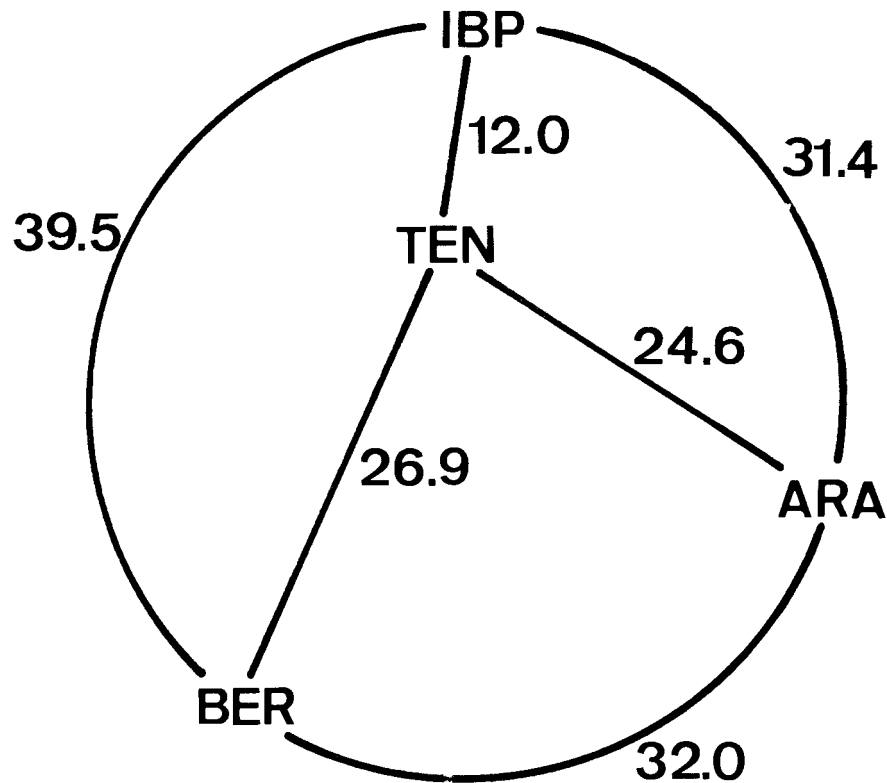


Fig. 2. Genetic relationships between populations of Tenerife (TEN), Iberian peninsula (IBP), and north African Arabs (ARA) and Berbers (BER). Figures indicate average genetic distances $\times 10^3$.

Middle East (Chibani et al., 1985; Cleve et al., 1992) are remarkable. Differences with Tuaregs and Algerians (Constans et al., 1980) are greater, in spite of their geographical proximity, and are most extreme with west Africans.

PI system. A low frequency for PI*M1 (0.528) and high values for PI*M2 (0.190) and PI*S (0.144) alleles are the most striking features of Tenerife as compared to other Iberian peninsula populations (Table 2). For this marker, Tenerife appears clearly as one of the poles of the gradient described in Europe for PI*M and PI*S allele distribution (Fagerhol and Cox, 1981). Also remarkable divergences are present with north African and Middle East populations (Chaabani et al., 1984; Nevo and Cleve, 1991; Nevo et al., 1992). Greater differences occur with west African populations, which are characterized by extremely high frequencies of PI*M1.

ORM1 system. ORM1*F allele frequency in Tenerife (0.639) ranges within the variation found on the Iberian peninsula (Table 2) and among other Europeans (0.58–0.66; Sandiunenge et al., 1993). African population studies are very limited and only a few populations have been described: Libyans, Nigerians and south African Zulus. Only the south African sample differs significantly from our population.

PLG system. The frequency of the PLG*A allele in the Tenerife population (0.745) is within the variation range for the Iberian peninsula as well as for other European populations (reviewed by Skoda et al., 1988, with data ranging from 0.64 to 0.84). In north African populations, only data for Libyans are reported with a significantly lower value (Table 3). In contrast, the PLG*A value for west Africa (Gambia [Skoda et al., 1988]) is significantly higher than in Tenerife (Table 3).

Comparison between populations

To investigate the genetic position of the Canarian population, we have selected several groups from the Iberian peninsula, to take into account the possible variation among different geographical areas. Unfortu-

nately, complete information was available for only the two main ethnic groups, Berbers and Arabs in north Africa. To enlarge the population context, other populations, such as those from France and west sub-Saharan Africa, were considered. Data were obtained for a total of 12 genetic systems and 46 alleles. Most of the data collected come either from our database on Iberian peninsula populations or are compilations (Mourant et al., 1976; Roychoudhury and Nei, 1988; Cavalli-Sforza et al., 1994).

For the protein data given here, the chi-square heterogeneity values between the population of Tenerife and the other groups (Table 2) which show the greatest differences are, in descending order: west Africa (5 out of 6 values are significant), north Africa, France, and the Iberian peninsula. The greatest number of differences were found for the PI system, due mainly to the low frequency of the PI*M1 allele in Tenerife populations compared to that of Iberians, and the high value of the PI*S in Tenerife compared to values for this allele in the non-peninsular populations.

Genetic distances. Pairwise Reynolds' distances between the 11 populations based on the protein loci studied and 12 classical polymorphisms are shown in Table 4. These measures show a strong correlation with those obtained by two other different methods (data not shown). All estimated distances are highly consistent according to the low relative values of their bootstrap standard errors. In all cases, 1.96 times the values of the standard errors are remarkably lower than the distance estimates. Both for protein and whole markers, the lowest genetic distances correspond to intra-Iberian peninsula comparisons (average distance values of 8.63 for proteins and 7.86 for all systems), and in general, among the European populations, whereas the highest distances appear, as it would be expected, between the sub-Saharan population and the remaining groups. A third group of intermediate values comprises distances be-

Fig. 3. Neighbor-joining tree relating populations. Abbreviations are given in Figure 1. Numbers indicate percentages of each splitting.

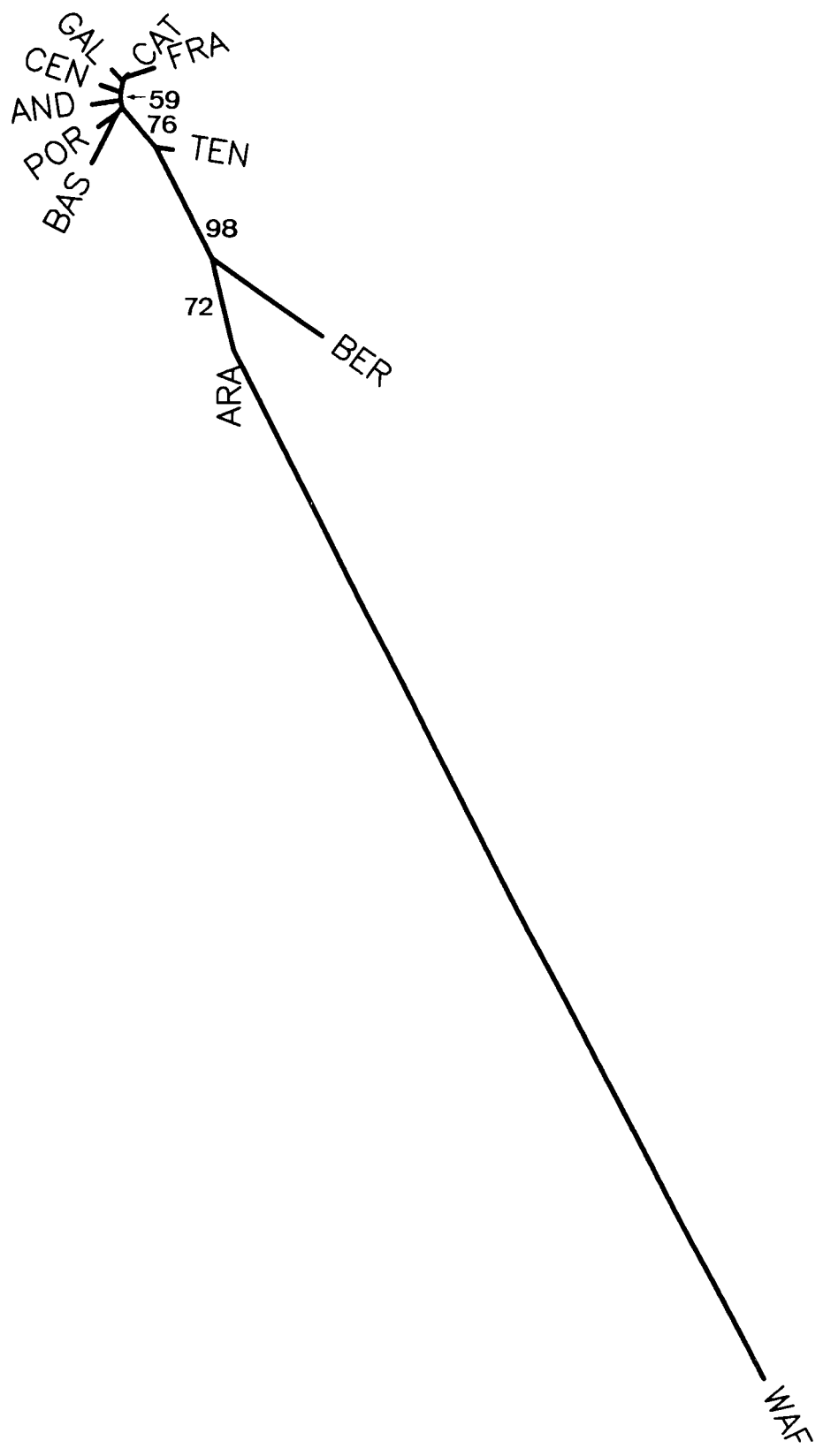
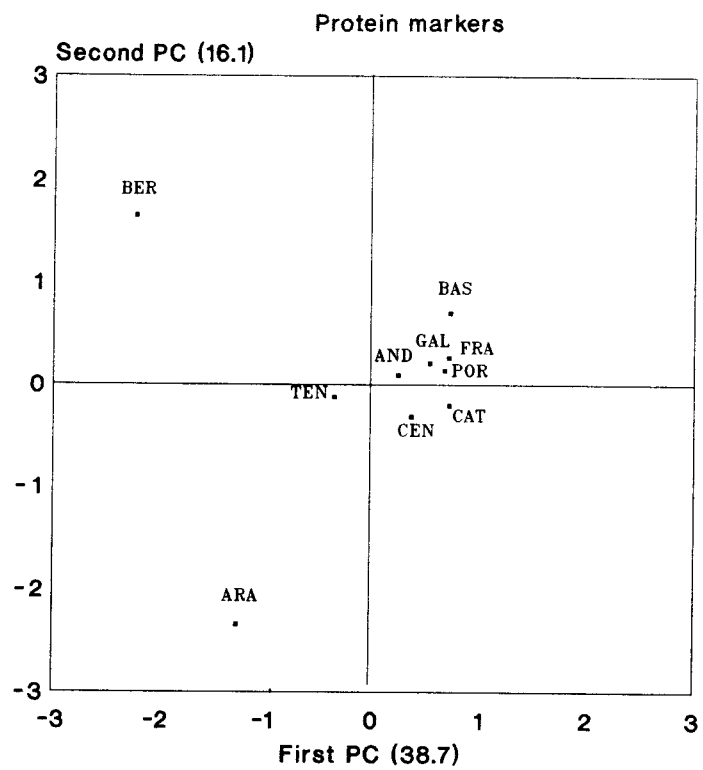
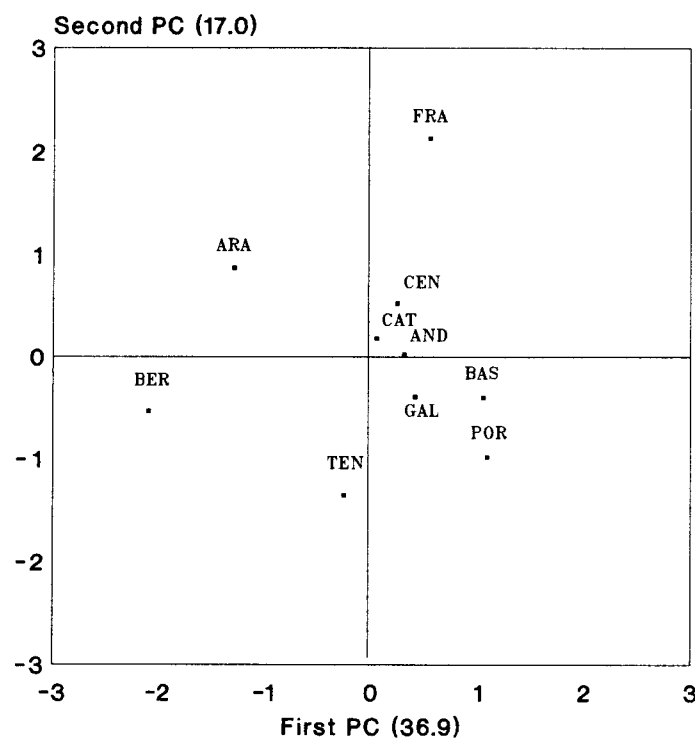


Fig. 3.



all systems

Fig. 4.

tween Europeans and the north African populations.

As for the genetic relationships between the populations of the Canary Islands, the Iberian peninsula and north Africa, Tenerife is closer to the Iberian peninsula than to other groups for all parameters, although the Tenerife-Iberian peninsula genetic differentiation is slightly higher than among Iberian groups (average values: 12.6 vs. 8.6 for proteins, and 12.0 vs. 7.9 for all systems). Between Tenerife and north African groups, some discrepancies were observed for proteins and all systems. For protein polymorphisms, the population of Tenerife was as close to Berbers (14.9) as to Iberian groups (12.6) and about twice the distance from the Arabs (25.2). This is precisely the opposite distance pattern apparent between Iberian peninsula and north African groups (average values of 22.4 from Berbers and 17.5 from Arabs). However, when all systems are considered, the Tenerife population is almost equidistant from Berbers (26.9) and Arabs (24.6). These distances are lower than those between Iberian peninsula-north Africans (average values of 39.5 with Berbers and 31.4 with Arabs) and Berbers-Arabs (32.0), and suggests that Tenerife is closer to north African populations than are Iberian peninsula groups. The genetic position of Tenerife midway between Berbers and Arabs and closer to Iberian peninsula populations than to north Africans is illustrated in Figure 2.

Distance relationships based on all systems are shown graphically by the 11 population neighbor-joining (NJ) tree in Figure 3. The topology of the tree consists of two major branches composed of African groups (bottom) and Europeans including Tenerife (top). Basically the same topology is displayed by an average linkage or UPGMA tree differing only in the order of branching among European groups (data not shown). The NJ tree highlights the extreme separation of west African as well as the fact that all African groups form one cluster with the

strongest statistical support (98%) from the available data. Tenerife is joined to this cluster in 76% of the bootstrap trees, which emphasizes the intermediate position of the Canarian population in relation to north Africans and Europeans.

Principal components. The results of principal component analysis for proteins and all systems is shown in Figure 4. Sub-Saharan populations were not included to get a clearer picture of the relationships among the European and north African groups. The first three components explain 68.2% (proteins) and 65.2% (all systems) of the total variance. For proteins, the population distribution on the first component separates Europeans from north Africans, whereas the second contributes primarily to the separation of the European groups. Here, Tenerife lies slightly outside the Iberian peninsula cluster in the direction of north Africans. The main gene contribution to this population distribution corresponds to the alleles TF*C2, GC*2, TF*C3, GC*1F, PI*S, and TF*C1 which are highly correlated ($r > 0.75$) with the first component. For all systems, the first component underlies the same main population subdivision between north Africans and Europeans as well as the peripheral position of Canarians in relation to the Iberian peninsula groups. The alleles PGD*A, RH*cDe, GC*2, TF*C2 and AB0*A1 show the strongest correlation ($r > 0.85$) with the first component. There is a substantial differentiation between Arabs and Berbers, while the European groups remain in an intermediate position as revealed by the second component.

Genetic admixture. Based on genetic distances, the admixture level of the Canary population with Europeans and north African groups was estimated according to Cavalli-Sforza's formula (1994). Assuming that the parental populations were Europeans (mainly from the Iberian peninsula) and Berbers, the contribution of Europeans yields a value of $m = 0.678$, and a very similar value ($m = 0.688$) is obtained when Europeans and Arabs are considered as parental groups. When Europeans and sub-Saharans

Fig. 4. Plots of the first two principal components (PC) for protein markers and all systems. Abbreviations are given in Figure 1.

are considered, the contribution of the latter to Canarians is around 6%.

DISCUSSION

The data examined emphasize the genetic similarity of present-day Canarians to the populations of the Iberian peninsula as shown by genetic distances and principal component analysis. The genetic contribution from the latter was estimated at about 70%. This similarity is in keeping with the historic record which shows an almost complete replacement of the indigenous population after the conquest of the islands by Spaniards in the 15th century.

In spite of an overall similarity, the Canarian population shows a certain degree of differentiation from Iberian populations, as illustrated by the extreme values of several protein frequencies in relation to Iberian variation ranges, and the relative graphic distance in the neighbor-joining tree and principal component representations. This differentiation could be interpreted as: (1) a bias in the origin of the conquering population; (2) a random local microdifferentiation due to the isolation, and (3) a result of mixture with other populations. The fact that this differentiation always tends towards north African characters points to a particular relationship with north African groups. These groups, Arabs and Berbers, show clear and similar genetic differentiations both between themselves and with the Iberian peninsula groups. Yet, the genetic separation of these two African groups from the Canarian population is similar in both cases and lower than that between themselves. These results would support the hypothesis of a non-Berber north African contribution to the Canarian gene pool which could be as important as the accepted Berber contribution. If this were the case, the Arab contribution would have had to have been introduced by north African slaves, brought to the Canary Islands after the Spanish conquest. Arabs settled in north Africa between the 7th and 11th centuries, and there is no evidence (historical, linguistic, archaeological, etc.) of the presence of this population group in the Canary Islands prior to the arrival of the Spanish.

Is it still not known whether the Berber contribution to the present-day population can be attributed to the remains of the original Guanche population, presumably related to the Berbers, or to the slave trade, as seems to be the case with the non-Berber contribution. The genetic information examined here does not allow us to discriminate between these two possibilities, but the amount of Guanche substrate would probably be no greater than the Arab slave contribution.

In conclusion, genetic data from classical polymorphisms show that the genetic composition of the present Canary population is largely similar to that of Iberian peninsula groups with some north African contributions (Berber and non-Berber) as well as minimal proportions of sub-Saharan genes. This fact contrasts with the much greater geographic proximity between Canary Islands and north Africa than with the Iberian peninsula and could suggest a higher isolation since colonization by the Spanish than one might expect, given the geographic distances involved.

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LITERATURE CITED

- Abercromby J (1917) A study of the ancient speech of the Canary Islands. In O Bates (ed.): *Varia Africana* (Harv. Afr. Stud. I). Cambridge, Mass.: Peabody Museum.
- Brown JKM (1994) Bootstrap hypothesis tests for evolutionary trees and other dendrograms. *Proc. Natl. Acad. Sci. USA* 91:12293-12297.
- Cavalli-Sforza LL, Edwards AWF (1967) Phylogenetic analysis: models and estimation procedures. *Am. J. Hum. Genet.* 19:233-257.
- Cavalli-Sforza LL, Menozzi P, and Piazza A (1994) *The History and Geography of Human Genes*. Princeton, NJ: Princeton University Press.
- Cavalli-Sforza LL, and Piazza A (1975) Analysis of evolution: Evolutionary rates, independence, and tree-ness. *Theor. Popul. Biol.* 8:127-165.
- Chaabani H, Martin JP, Frants RR, and Lefranc G (1984) Genetic study of Tunisian Berbers. II. Alpha₁-antitrypsin (Pi) polymorphism: Report of a New allele (Pi S Berber). *Expl. Clin. Immunogenet.* 1:19-24.
- Chibani J, Lefranc G, and Constans J (1985) Serum polymorphisms among Tunisian Berbers: Haptoglo-

- bin, transferrin and group-specific component subtypes, C3 and BF types. *Ann. Hum. Biol.* 12:449-462.
- Cleve H, Koller A, Patutchnick W, Rodewald A, and Nabulsi A (1992) Genetic serum protein polymorphisms in Jordanian Arabs: A pilot study of the systems AHSG, BF, FXIII B, GC, PI, PLG and TF. *Gene Geography* 6:31-40.
- Constans J, Richard P, and Viau M (1978) Relationship between Hp^{1S} and Hp² gene frequencies among human populations. *Hum. Hered.* 28:328-334.
- Constans J, Lefevre-Witier P, Richard P, and Jaeger G (1980) Gc (vitamin D-binding protein) subtype polymorphism and variants distribution among Saharan, Middle East, and African populations. *Am. J. Phys. Anthropol.* 52:435-441.
- Constans J, Viau M, Gouillard C, and Clerc A (1981) Haptoglobin polymorphism among saharan and West African groups: Haptoglobin determination by radio-immuno-electrophoresis on HpO samples. *Am. J. Hum. Genet.* 33:606-616.
- Crosby AW (1986) *Ecological imperialism. The Biological Expansion of Europe, 900-1900.* Cambridge: Cambridge University Press.
- Efron B (1982) *The Jackknife, Bootstrap, and Other Resampling Plans.* Philadelphia, PA: Society for Industrial and Applied Mathematics.
- Fagerhol MK, and Cox DW (1981) The PI polymorphism: Genetic, biochemical and clinical aspects of human alpha-1-antitrypsin. *Adv. Hum. Genet.* 11: 1-62.
- Felsenstein J (1989) PHYLIP—Phylogeny Inference Package (version 3.2). *Cladistics* 5:164-166.
- Fischer E (1931) Sind die alter Kanarier ausgestorben? *Z. F. Ethnol.* 62:258-281.
- Fusté M (1959) Contribution à l'anthropologie de la Grande Canarie. *L'Anthropologie* 63:295-318.
- Fusté M (1962) Diferencias antropogeográficas en las poblaciones de Gran Canaria. *Anuario de Estudios Atlánticos (Madrid-Las Palmas)* 8:67-86.
- Fusté M (1965) Physical Anthropology of the Canary Islands. *Am. J. Phys. Anthropol.* 23:285-292.
- Kahlich-Könner D, Mayr WR, Prokop O, and Weninger M (1969) Erythrocyten-und serummerkmalen bei den einwohnern der Kanarischen inseln. *Anthropol. Anz.* 31:181-183.
- Kamboh MI, and Ferrell RE (1986) Ethnic variation in vitamin D-binding protein (GC): A review of isoelectric focusing studies in human populations. *Hum. Genet.* 72:281-293.
- Kamboh MI, and Ferrell RE (1987) Human transferrin polymorphism. *Hum. Hered.* 37:65-81.
- Moral P, Marogna G, Salis M, Succa V, and Vona G (1994a) Genetic data on Alghero population (Sardinia): Contrast between biological and cultural evidence. *Am. J. Phys. Anthropol.* 93:441-453.
- Moral P, Vives S, Fisac R, Martín J, and Mesa MS (1994b) Serum protein polymorphisms (HP, TF-, GC- and PI subtypes) in two mountain communities of Sierra de Gredos (Central Spain). *Gene Geography* 8:215-222.
- Morilla JM, Afonso JM, Hernández M, Pestano JJ, and Larruga JM (1988) Human enzyme polymorphism in the Canary Islands. II. African influence. *Hum. Hered.* 38:101-105.
- Mourant AE, Kopeć AC, and Domaniewska-Sobzak K (1976) *The Distribution of the Human Blood Groups and Other Polymorphisms.* London: Oxford University Press.
- Nei M (1972) Genetic distance between populations. *Amer. Natur.* 106:283-292.
- Nevo S, and Cleve H (1991) The PI polymorphism in Israel: Report of six Jewish population groups. *Am. J. Med. Genet.* 39:1-6.
- Nevo S, Cleve H, Koller A, Eigel E, Patutchnick W, Kanaaneh H, and Joel A (1992) serum protein polymorphisms in Arab Moslems and Druze of Israel: BF, F13B, AHSG, GC, PLG, PI and TF. *Hum. Biol.* 64:587-603.
- Onrubia-Pintado J (1987) Les cultures préhistoriques des Iles Canaries. Etat de la question. *L'Anthropologie* 91:653-678.
- Piazza A, Olivetti E, Barbanti M, Reali G, Domanici R, Giari A, Benciolini P, Caezzano L, Cortivo P, Bestetti A, Bonavita V, Crino C, Pascali VL, Fiori A, and Barbagna M (1989) The distribution of some polymorphisms in Italy. *Gene Geography* 3:69-139.
- Pinto F, Cabrera VM, González AM, Larruga JM, Noya A, and Hernández M (1994) Human enzyme polymorphism in the Canary Islands. VI. Northwest African influence. *Hum. Hered.* 44:156-161.
- Pons J, Fusté M, Diaz JM, and Planas J (1968) Haptoglobin types in the population of Gran Canaria. *Acta Genet. Stat. Med.* 18:579-583.
- Reynolds J, Weir BS, and Cockerham CC (1983) Estimation of the coancestry coefficient: Basis for a short-term genetic distance. *Genetics* 105:767-779.
- Roberts DF, Evans M, Ikin EW, and Mourant AE (1966) Blood groups and the affinities of the Canary islanders. *Man* 1:512-525.
- Roychoudhury AK, and Nei M (1988) *Human Polymorphic Genes. World Distribution.* Oxford: Oxford University Press.
- Saha N, and Banerjee B (1986) A study of some blood characteristics of Bedouin and non-Bedouin Arabs of Jordan. *Hum. Hered.* 36:276-280.
- Saitou N, and Nei M (1987) The neighbor-joining method: A new method for reconstructing phylogenetic trees. *Molec. Biol. Evol.* 4:406-425.
- Sandiumenge T, Vives S, and Moral P (1993) Orosomucoid and haptoglobin polymorphisms in two Spanish Pyrenean populations. *Gene Geography* 7:243-250.
- Schwidetzky I (1963) La población prehispánica de las Islas Canarias. *Investigaciones antropológicas. Sta. Cruz de Tenerife (Spain) Publ. del Museo Arqueológico de Tenerife* 4:217.
- Sebetan IM (1991) Plasminogen polymorphism in Libyans: Description of a new rare variant. *Hum. Hered.* 41:138-140.
- Sebetan IM, Sagisaka K (1988) Genetic polymorphism of orosomucoid ORM1 and ORM2 in Libyans: Occurrence of *ORM1**2.1 and three new ORM2 alleles. *Jap. J. Hum. Genet.* 33:439-443.
- Skoda U, Klein A, Lübecke I, Mauff G, and Pulverer G (1988) Application of plasminogen polymorphisms to forensic haemogenetics. *Electrophoresis* 9:422-426.
- Verneau R (1887) Rapport d'une mission scientifique dans l'Archipel canarien. *Archives des Missions Sc. et Litté. 3^e sér. XVIII*:567-817.
- Walter H, Arndt-Hanser A, Raffa M, and Gumbel B (1975) On the distribution of some genetic markers in Libya. *Humangenetik* 27:129-136.
- Wolfel DJ (1930) Sind die ureinwohner der Kanaren ausgestorben? *Z. Ethnol.* 62:282-302.
- Wolfel DJ (1955) *Eurafrikanische worstschichten als kulturschichten.* Salamanca University (Spain) *Acta Salmant.* 9.